Phenotyping progenies for complex architectural traits: a strategy for 1-year-old apple trees (Malus x domestica Borkh.)

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ABSTRACT

The aim of this study was to define a methodology for describing architectural traits in a quantitative way on tree descendants. Our strategy was to collect traits related to both tree structural organization, resulting from growth and branching, and tree form and then to select among these traits relevant descriptors on the basis of their genetic parameters. Because the complexity of tree architecture increases with tree age, we chose to describe the trees in the early stages of development. The study was carried out on a one-year-old apple progeny derived from two parent cultivars with contrasted architecture. A large number of variables were collected at different positions and scales within the trees. Broad sense heritability and genetic correlations were estimated and the within tree variability was analyzed for variables measured on long sylleptic axillary shoots (LSAS). These results were combined in order to select heritable and not correlated variables. Finally, the selection of variables proposed combines topological with geometric traits measured on both trunks and LSAS: (i) on the trunk, mean internode length and number of sylleptic axillary shoots; (ii) on axillary shoots, conicity, bending and number of sylleptic axillary shoots born at order 3. The trees of the progeny were partitioned on the basis of these variables. The putative agronomic interest of the selected variables with respect to the subsequent tree development is discussed.

INTRODUCTION

Apple breeding programs aim primarily to develop productive cultivars with good fruit quality, and ensure pest and disease resistance (Lespinasse 1992). But, the consideration of tree architecture and shoot morphology traits is also considered as a promising manner to obtain trees that are adapted to training systems while reducing intrants and improving the control of vegetative development and yield regularity (Lespinasse 1992; Laurens et al. 2000). Usually, the introduction of traits which segregate in a quantitative way in selection schemes requires genetic studies to analyse their variability and to estimate the expected genetic improvement (Gallais 1989; Hill et al. 1998). To investigate the relationship between traits measured and genotypic effect, the concept of heritability has been introduced into quantitative genetics (Hanson 1963; Falconer 1981). However, accurate heritability estimates can be obtained only if it is possible to extend the phenotyping to many trees (Yao and Mehlenbacher 2000; Hardner et al. 2002; Chao and Parfitt 2003; Liebhard et al. 2003).

Great variability in tree habit has been demonstrated in apple cultivars, which have been qualitatively classified into 4 architectural types according to tree growth habit, distribution of branches and fruiting position (Lespinasse 1977). In the 1970s, the discovery of natural mutants with a columnar compact growth habit (Lapins 1974; Lapins 1976) led Lespinasse (1992) to modify this classification:.Type I is now composed of columnar cultivars (e.g. ‘Wijcik’); Type II is characterized by erect trees that mainly bear short shoots and by fruiting on spurs with alternate bearing (e.g. ‘Starkrimson’); Type III is composed of cultivars with medium to long shoots and an open branching angle (e.g. ‘Golden Delicious’); Type IV is characterized by weeping trees that mainly bear long shoots and by fruiting on medium and long shoots and production that is usually regular (e.g. ‘Granny smith’). Tree form can also be evaluated through the overall tree hierarchic organisation, using the concepts of hierarchy vs. polyarchy introduced by Edelin (1991)

and used to described two-year-old apple trees (De Wit et al. 2004). However, studies based on qualitative classification of the trees into types without precise and objective measurements may, as Hansche et al. (1972) argued, induce large errors in the estimation of genetic parameters. Over the last ten years more detailed architectural studies have been performed in different species, with a distinction between tree topology (i.e. relative position of the entities within the tree) and geometry (i.e. spatial position and form of the entities), and considering entities at different scales (Godin et al. 1999a). Regarding the topological organization in apple tree, the variability of branching patterns has been investigated for several cultivars along branches (Lauri et al. 1995) and trunks (Costes and Guédon 2002). Tree and branches form has also been investigated. A modeling approach carried out on three contrasted varieties of apricot tree, showed that the main factors involved in the final shoot form were first its initial geometry (in particular slenderness and inclination) and second the distribution of load along the shoot (Alméras et al. 2004). But these studies were performed on contrasted cultivars and genetic parameters of traits have not been investigated.

Regarding genetic studies for architectural traits in apple tree, accurate values of heritability have been estimated by studying several full-sib progenies, but only basic morphological traits such as trunk diameter were investigated (Tancred et al. 1995; Durel et al. 1998; Oraguzie et al. 2001). Recently Liebhard et al. (2003) estimated genetic and environmental variances and highlighted QTLs for growth (tree height and basis diameter) and phenological traits in an apple progeny. However, most of the genetic studies have been performed on the inheritance of the columnar trait suggesting that a single dominant gene called Co was implicated (Lapins 1974; Lapins 1976). Several genetic maps were drawn up for apple progenies deriving from a columnar parent and molecular markers close to the Co gene were found (Hemmat et al. 1997; Kim et al. 2003). Gradually, tree architecture was investigated in more depth and took account of more complex characters,

96 in particular the branching process: (i) long shoots were shown to be relevant for
97 partitioning adult trees belonging to a progeny derived from ‘Wijcik’ (type I) and ‘Baujade’
98 (type IV) (Godin et al. 1999b); (ii) main shoot growth and its branching characteristics
99 were used to cluster a 1-year-old progeny deriving from ‘Telamon’ (type I) and ‘Braeburn’
100 (type III) (De Wit et al. 2002). But these studies did not investigate the genetic variability
101 of traits. In addition, the Co gene was shown to have pleiotropic effects and could thus hide
102 the variability of other architectural traits (Kenis and Keulemans 2004).

103 This study aimed at defining a method to describe tree architecture based on
104 accurate and objective measurements which remain compatible with quantitative genetic
105 studies carried out with large progenies and open new perspectives on Quantitative Traits
106 Loci (QTL) research. In particular, the perennial structure of trees induces methodological
107 difficulties in the phenotyping for architectural traits (Osorio et al. 2003; Jansson et al.
108 2005). Indeed, a diminution in primary growth in relation to tree age has been showed for
109 different species and in different agronomic contexts (Barthélémy et al. 1997; Costes et al.
110 2003; Seleznyova et al. 2003). Because of these gradients, the successive years cannot be
111 used as repetitions to separate genotype and environment effects. Furthermore, some traits
112 are only transiently expressed in the course of tree development (e.g. sylleptic branching
113 mainly expressed early before tree maturity is reached) while others are cumulated over
114 years (primary and secondary growth). To account for these difficulties, we chose to start
115 phenotyping the trees from the first year of growth when the structure is simple enough to
116 investigate a large number of traits, measured on a large number of trees. This allowed us
117 to consider both the topology and geometry of entities, at different positions and scales
118 within the trees. The following questions were addressed: (i) which variables should be
119 measured to point out the architectural variability ? (ii) should we measure either trunks or
120 long sylleptic axillary shoots (LSAS) or both ? (iii) if LSAS have to be considered, how
121 many should be measured per tree ? Among the large number of variables explored we then

made a selection based on the three following criteria: (i) high heritability value (ii) low genetic correlations between selected variables, and (iii) putative agronomic interest and easiness of measurement.

MATERIALS AND METHODS

Plant Material

The progeny under study was derived from a 'Starkrimson' x 'Granny Smith' cross. Parents were chosen for their contrasting architecture. According to Lespinasse (1992), the 'Starkrimson' maternal parent has an erect growth habit with many short shoots and a tendency to irregular production (type II). The 'Granny Smith' pollen parent is characterized by a weeping growth habit with long shoots and fruit bearing regularity (type IV).

In 2002, 125 seedlings were grown on their own roots for one year. At the beginning of 2003, grafts were taken on 3 successive nodes in the middle of the shoots from 50 plants selected at random. Three grafts were carried out for each of the 50 genotypes onto 'Pajam 1' rootstock to produce repetitions. Rootstocks were bought to nursery men and selected for their uniformity. 'Pajam 1' rootstock is a clonal selection of M9 which confers low vigor, a short juvenile period and substantial, regular productivity. The 150 trees obtained were planted in March 2003 at the Melgueil INRA Montpellier experimental station 5m x 2m apart in an east - west orientation. In order to study their architecture, the trees were grown with minimal training, i.e. trees were not pruned and the trunks were staked up to 1 m. They were regularly irrigated using a microjet system to avoid soil water deficits. Pests and diseases were controlled by conventional means in line with professional practices throughout the study.

Morphological and Architectural Description

A total of 149 trees were observed in January 2004 after the first year of growth (one tree had died). At that time, the trees were composed of a trunk, sometimes with rhythmic growth (i.e. meristem activity was periodic), and sylleptic axillary shoots (Figure 1). Three types of sylleptic axillary shoot were distinguished depending on their length: (i) long shoots (length $\geq$ 20 cm); (ii) brindles (5 cm $\leq$ length $<$ 20 cm); spurs (length $<$ 5cm). For

each of the 149 trees, observations were performed on the trunk and 4 long sylleptic axillary shoots (LSAS) when present. This led us to consider unbalanced dataset on LSAS.

A topological description of the trees was established using the coding method defined by (Godin et al. 1997). Four organization levels were distinguished, first the tree, second the axes, third the growth units (GU) and fourth the internodes. A geometrical description was based on the following variables: (i) length measured at the GU level; (ii) basis and top diameters measured on the trunk and LSAS; (iii) basis and top angles, cord measured on LSAS (Figure1).

These measured variables were used to calculate others aiming to provide descriptors as close as possible to biological processes such as internodes lengthening or bending. These calculations and further analyses were performed with AMAPmod software (Godin and Guédon 2003). Variables were divided into 2 categories whether they were related to tree geometry or to topology. Topological variables were organized into growth and branching variables (Table 1).

Statistical analysis

Broad sense heritability (h^2_b) has been defined as the ratio between genotypic variance and phenotypic variance (Hanson 1963):

$$h^2_b = \frac{\sigma^2_G}{\sigma^2_P}$$

Where: σ^2_G is genotypic variance, σ^2_P is phenotypic variance.

If phenotypic variance is broken down into genetic variance and environmental variance, then broad sense heritability is given by:

$$h^2_b = \frac{\sigma^2_G}{(\sigma^2_G + \sigma^2_e)}$$

Where: $\sigma^2 e$ is error variance as an estimation of environmental variance.

As several LSAS were described on each tree, the mean value per tree was used to estimate individual heritability, i.e. at the level of the individual, while on trunks the measured values were used directly. The restricted maximum likelihood method (REML) (Corbeil and Searle 1976) was used to estimate both “genotype” and “error” variances since it is considered the most suitable procedure to estimate variance components for unbalanced data (Dieters et al. 1995). Individual broad sense heritability values were then calculated along with the associated standard deviations to obtain a confidence interval for the estimates (Agresti and Coull 1998). According to Gallais (1989), variables are considered as heritables if (i) their heritability value is greater than 0.2; (ii) the lower limit for the confidence interval of their heritability value is greater than 0. Within-tree variability was also estimated for variables measured on the LSAS in addition to the genotypic and error variances, and this to evaluate the stability of the variables within the trees. Moreover, in order to determine the minimal number of LSAS which should be described to obtain accurate values of individual broad sense heritability, this parameter was calculated by considering an increasing number of LSAS, from 1 to 4.

Then, relevant traits were selected to match 2 criteria. The first selection criterion was the broad sense heritability of traits and the associated confidence interval. The second was the genetic correlation between characters, since two variables with a significant genetic correlation can be predicted one from the other, and this allows the breeder to use only one variable, e.g. the easiest to measure (Gallais 1989). Genetic correlations were calculated between the variables using the average value by genotype (Hill 1971).

In order to define groups of trees with relatively similar architectures, the trees were partitioned for trunk and axillary shoot traits using the Partitioning Around Medoids (PAM) method (Kaufman and Rousseeuw 1990). Partition was performed on the relevant selected traits because we wanted to consider only heritable variables. Partition quality was evaluated by (i) the ratio between global within-cluster distance and global between-cluster

200 distance, and (ii) the partition mean silhouette value (S_{mean}) (Kaufman and Rousseeuw
201 1990). The higher the S_{mean} value, the more separated the clusters. Cluster isolation was
202 evaluated by (i) their diameter i.e. dissimilarity between the most dissimilar object of a
203 cluster and (ii) their separation i.e. smallest dissimilarity between an object in the cluster
204 and an object outside the cluster. Partitioning was performed from the dissimilarity matrix
205 between trees (Kaufman and Rousseeuw 1990). Euclidean distances between trees were
206 calculated from standardized data. For non branching trees, missing data for axillary shoots
207 were replaced by the mean value for the variable. Finally, to investigate how the variables
208 discriminated each cluster, an ANOVA study and a Newman and Keuls test were carried
209 out between clusters.

210 Genetic correlations and genetic models of variance decomposition used to
211 calculate h^2b were performed using Proc Corr and Proc Mixed respectively in SAS v8
212 software (SAS Institute Inc 2000). Partitioning methods were those in the stat module of
213 AMAPmod software (Godin and Guédon 2003). ANOVA and Newman and Keuls tests
214 used to investigate the differences between clusters were performed using Proc GLM in
215 SAS v8 software.
216

RESULTS

Broad sense heritability of traits

The geometrical variables measured on the trunks showed relatively low heritability values (Table 2). Among them, the highest values were found for variables related to the trunk length: length (L), mean internode length (IN_L), length of the longest internode (IN_L_max) and slenderness (Slend). All these variables had heritability values greater than 0.2 and the lower limit of their confidence interval was in excess of 0.1. Three branching variables showed high heritability values close to 0.4 and the lower limit of their confidence interval was greater than 0.2: number of axillary shoots (Nb_AS), number of spurs (Nb_S) and branching by length unit (Nb_AS/L).

Among the geometrical variables measured on LSAS, those which characterized internode length (IN_L, IN_L_max) and shoot conicity (Coni) showed the highest heritability values (0.5 and 0.4 respectively), and the lower limit of their confidence interval was greater than 0.2 (Table 2). Bending variables (Cord_Bend, Ang_Bend) and slenderness (Slend) showed intermediate values close to 0.3. In the same manner as for the trunks, many branching variables (Nb_AS, Nb_S, %AS, Nb_AS/L) measured on the LSAS were highly heritable (h^2_b close to 0.5, with the lower limit of the confidence interval close to 0.3).

By contrast, some volume-related variables (basis diameter – B_Dia, mean diameter – M_Dia and volume – Vol) and count-related variables (number of internodes – IN_N, number of long shoots – Nb_L, branching density – Br_D) showed low heritability values (h^2_b lower than 0.2) whether they were measured on trunks or the LSAS.

Within-tree variability of variables measured on the LSAS

A significant within-tree effect was observed for all geometrical variables (Table 3). But, several variables (mean internode length – IN_L, length of the longest internode – IN_L_max and cord bending – Cord_Bend) also showed genotypic variance that was

242 greater than the within-tree variance. Of the topological variables, some branching
243 variables, such as number of axillary shoots (Nb_AS), number of long shoots (NB_L),
244 number of brindles (Nb_B) or branching zone (Br_Z), were considered as stable because
245 they did not show a significant within-tree effect. Excepted the number of long shoots
246 (Nb_L), all these branching variables also showed a significant genotypic effect.

247 The individual broad sense heritability values were then estimated by considering
248 an increasing number of LSAS per tree. Depending on the variable, 3 kinds of patterns
249 were observed which are illustrated only for a selection of variables (Figure 2). The
250 heritability values increased with the number of LSAS for many branching variables (e.g.
251 number of axillary shoots – Nb_AS and number of brindles – Nb_B) and some geometrical
252 variables (e.g. Conicity – Coni). All these variables showed a highly significant genotypic
253 variance, while their within-tree variance was generally non significant or lower than the
254 genotypic variance (Table 3). By contrast, the heritability values decreased when the
255 number of LSAS considered increased for variables which showed a non significant
256 genotypic variance while their within-tree variance was significant to highly significant
257 (e.g. branching density – Br_D). In a third intermediate case, quite similar heritability
258 values were obtained whatever the number of LSAS considered. This case includes
259 variables with significant genotypic and within-tree variances (e.g. cord bending –
260 Cord_Bend). For most of the variables considered in the study, the highest difference in
261 heritability values was obtained between 1 and 2 LSAS considered (e.g. number of axillary
262 shoots – Nb_AS, conicity – Coni, branching density – Br_D) even though, in several cases,
263 the heritability value changed until 3 LSAS considered (e.g. number of brindles – Nb_B or
264 top angle – T_Ang).

265 ***Correlations between variables***

266 High phenotypic correlations were observed between the variables measured either on the
267 trunk or LSAS and highlighted a high level of redundancy (data not shown). Most of the

variables exhibited even higher genetic than phenotypic correlations. Significant genetic correlations were mainly observed between variables belonging to a same category, i.e. geometric or topological (Table 4). In fact, more than 80 % of the variables belonging to the same category showed significant genetic correlations on both trunks and LSAS. Significant genetic correlations were also observed between geometric and topological variables, for instance on trunks (i) between 2 variables that characterize growth: length (L) and number of internodes (IN_N) (r = 0.86); (ii) between a geometric and a branching variable: slenderness (Slend) and branching by length unit (Nb_AS/L) (r = - 0.55).

If the same variables are considered on both trunks and LSAS, most of the geometric variables, except slenderness (Slend) and conicity (Coni), showed strong genetic correlations one with the other (r ranged from 0.5 to 0.7). Topological variables showed significant genetic correlations for number of internodes (IN_N), number of axillary shoots (Nb_AS), number of spurs (Nb_S), percentage of branching nodes (%AS), number of axillary shoots by length unit (Nb_AS/L) and branching zone (Br_Z). However, these genetic correlations were fairly weak (r around 0.3) compared with the geometric variables.

Selection of relevant descriptors

High genetic correlations per category of variables make it possible to reduce redundancy and select variables that are representative of the different aspects of tree architecture, including both geometric and topological descriptors.

The geometric variables that characterize internode length (i.e. mean internode length – IN_L and length of the longest internode – IN_L_max) were the only ones to show elevate heritability values on both trunks and LSAS. Furthermore, mean internode length (IN_L) was more strongly correlated with other geometric variables than length of the longest internode (IN_L_max). We thus selected the mean internode length (IN_L) as a descriptor of trunk geometry. LSAS geometry was characterized by cord bending (Cord_Bend) and conicity (Coni) because: (i) their heritability values were high to

294 moderate; (ii) they showed a weak genetic correlation one with the other; (iii) they were not
295 correlated with mean internode length (IN_L) on the trunks (Table 4).

296 Branching variables were highly heritable on both trunks and LSAS. These
297 variables were strongly correlated one with the other when they were considered separately
298 either on trunks or LSAS. In particular, the number of axillary shoots (Nb_AS) showed a
299 strong genetic correlation with all the other branching variables measured on the same axis,
300 either trunks or LSAS. Besides, the within-tree variability for the number of axillary shoots
301 (Nb_AS) was not significant, unlike the number of spurs (Nb_S) and branching by length
302 unit (Nb_AS/L). Finally, a weak genetic correlation was observed between the number of
303 axillary shoots (Nb_AS) measured respectively on the trunks and on the LSAS (Table 4).
304 For all these reasons, the number of axillary shoots (Nb_AS) were selected as relevant
305 variables on both trunks and LSAS.

306 Thus, 5 variables were selected to describe both tree geometry and topology: (i) on
307 trunks, mean internode length (IN_L_tr) and the number of axillary shoots (Nb_AS_tr); (ii)
308 on LSAS, conicity (Coni_as), cord bending (Cord_bend) and the number of axillary shoots
309 born at order 3 (Nb_AS_as).

310 ***Partitioning the trees of the progeny***

311 The trees of the progeny were then partitioned on the basis of the mean standardized values
312 of the 5 selected variables. Several partitions were performed with the number of clusters
313 increasing from 2 to 8, called P_2 to P_8. The highest mean silhouette values were found for
314 partitions P_2 (S_{mean} = 0.38) and P_6 (S_{mean} = 0.22). These partitions were also characterized
315 by a ratio of 0.62 between global within-cluster dissimilarity and global between-cluster
316 dissimilarity. In P_2, the number of axillary shoots born at order 3 (Nb_AS_as) was the only
317 variable used for cluster discrimination (data not shown). In P_6, even though no clusters
318 were clearly isolated (i.e. for each one diameter was higher than separation), significant
319 differences were observed between clusters for all the 5 variables (Table 5). The first 3

clusters were discriminated by LSAS variables, i.e. the number of axillary shoots born at order 3 (Nb_AS_as), cord bending (Cord_Bend_as) and conicity (Coni_as) (Figure 3). These clusters were characterized by the lowest number of trees and the highest separation values. Clusters 4, 5 and 6 were composed of 39, 34 and 42 trees respectively and their separation values were fairly low. Clusters 4 and 5 were discriminated by trunk variables, i.e. branching (Nb_As_tr) and internode length (IN_L_tr), while cluster 6 was characterized by low values for all 5 variables. The distribution of trees in a given genotype between the clusters was investigated. 3 cases were observed: (i) the 3 replicates were in the same cluster; (ii) 2 replicates were in the same cluster; (iii) each replicate was in a different clusters. The proportion of genotypes observed in each case was respectively 24 % (12 genotypes), 52 % (26 genotypes) and 24 % (12 genotypes).

DISCUSSION AND CONCLUSION

Selecting quantitative variables : which method ?

The first criterion we used to select variables was broad sense heritability. A variance decomposition was performed using the REML method because it gives a confidence interval for heritability and is considered the most suitable procedure to estimate variance components for unbalanced data (Dieters et al. 1995). However, heritability estimates are specific to the population and the environment analyzed (Souza et al. 1998). In particular, the choice of the parents is crucial since their contrasted behaviour for a trait does not guarantee its segregation in the progeny. Indeed, when parents are both homozygous for a trait, then all the descendants display the same heterozygous genotype for this trait. However, in apple tree, cultivars are known to be very heterozygous. In addition, the quantitative distributions of the studied traits suggest a probable polygenic control and in this case the probability that all genes responsible for trait expression are homozygous for the two parents is very low. After due consideration of the above, the parents of the progeny were chosen for their contrasted architecture ('Starkrimson' is type II and 'Granny Smith' is type IV according to the Lespinasse classification (1992)). As a matter of fact, fairly elevated heritability values were obtained even though measurements repetitions, at least for a subset of variables, either on different progenies or different climatic conditions would complement the present results and lead to more precise trait selection.

The second criteria used for selecting variables consisted in taking account of within-tree architectural variability. Indeed plant structure results, at least to some extent, from repetitive processes (White 1979). In particular, branches belonging to a same apple tree exhibit similar behavior in growth, branching and flowering occurrence (Costes et al. 2003). In the present study, significant within-tree variability, as observed for many variables at the LSAS level, underlined the difficulty in characterizing individuals on the basis of a single value. Moreover, a more accurate estimate of heritability was obtained by

357 considering at least 2 repetitions of LSAS within the trees. This suggests that adequate
358 within tree sampling benefits to estimations of the genetic parameters. Even though in
359 some cases heritability values would be still over or under estimated, the choice of 2 LSAS
360 described by tree appears as a realistic compromise between the time of notation required
361 and the accuracy of the heritability value.

362 A third criteria was the analysis of genetic correlations between variables which
363 highlighted, as expected, a high redundancy among variables. This analysis avoid to select
364 among the variables *a priori* in a relative speculative way. Rather, it led us to select
365 variables in each group of highly correlated traits, with a minimum of correlations between
366 them. In addition, genetic correlations provide information on the other variables which
367 could be predicted from the selected variables (Gallais 1989), when correlation between the
368 variables considered explains a sufficient part of variance. For instance, the high genetic
369 correlations between the mean internode length considered on trunks and many geometrical
370 variables measured on both trunks and LSAS, suggests that this variable should be
371 representative of axis geometry in trees.

372 These criteria allowed us to select relevant traits which were used for partitioning
373 progeny into architectural groups containing trees of relatively similar branching and form.
374 The PAM method was used rather than more classical methods such as hierarchic
375 classifications, because it gives a small number of clusters containing a large number of
376 individuals, and it provides a wealth of statistics to evaluate the clustering stability, and
377 thus choose the more stable partition (Kaufman and Rousseeuw 1990). The partitioning
378 into 6 clusters on the basis of these statistics took account of all tree architecture since both
379 branching and geometrical variables were considered on both trunk and LSAS. Moreover,
380 since variables with fairly elevated heritability values were selected for the partition, more
381 than 75% of genotypes had at least two repetitions in the same cluster. This objective
382 partitioning could be used to test simplified tree phenotyping when screening juvenile trees

383 in a nursery. Such a partitioning could be useful in progenies that lack major genes such as
384 Co involved in the cross, i.e. when no contrasted phenotypes can be visually identified
385 down the rows.
386 ***Which relevance of the proposed variables with respect to further tree development ?***
387 Basic morphological traits in the apple tree, such as basis diameter and length, are usually
388 measured to characterize the trunk "vigor". In previous studies, heritability values for trunk
389 basis diameter were close to 0.5 (Durel et al. 1998; Liebhard et al. 2003). Our results seem
390 to underestimate the genetic variability for this variable with an heritability value of 0.12.
391 In the same manner our result seems to underestimate heritability for trunk height since
392 Watkins and Spangelo (1970) showed high additive variance for this trait. This low value
393 may be due to a lack of contrast between the progeny parents for this trait (as previously
394 discussed), or a reduction in total variability because of a rootstock effect. In support of
395 this, the studies conducted by Watkins and Spangelo (1970) and Durel et al. (1998) were
396 carried out with trees on their own roots, and the 'Fiesta' and 'Discovery' parents of the
397 progeny studied by (Liebhard et al. 2003) were considered as contrasted for this character.
398 Regarding trunk height, our results were consistent with the study of Liebhard et al. (2003)
399 performed on a progeny grafted on low vigorous rootstock (M27), since we calculated an
400 heritability value of 0.38 for trunk length. However, we selected a more local trait, i.e.
401 mean internode length, to represent trunk geometry as it was considered as the most
402 relevant. Thus, more global descriptors such as shoot length, made up of a combination of
403 both internode length and number of internodes, appears as less convenient for our purpose.
404 Moreover, this suggests that the emergence of new metamers (i.e. the elementary set of
405 organs from which a plant is built (White 1979)) is a process which allows the plant to
406 adapt to its environment and contribute to its architectural plasticity whereas internode
407 lengthening appears as a more stable process. However, internode length is likely to depend

on the agronomic context, e.g. rootstock (Seleznyova et al. 2003) and should be further investigated.

Previous studies have considered few variables of axillary shoot morphology. Axillary shoot length was used to cluster 'Telamon' x 'Breaburn' progeny (De Wit et al. 2002). But this variable is not significantly affected by genotype and consequently had a low heritability value in the present study. As previously discussed for trunk length, this is probably due to the combination of both internode lengthening and the leaf emergence process. An analysis of genetic parameters in the progeny under study showed that the most relevant traits on axillary shoot geometry consisted of conicity and cord bending. These variables had a substantial impact on progeny clustering since they separated 2 clusters containing a fairly low number of trees and characterizing by a quite high separation value. From an agronomic point of view, the flexion of branches is an important factor in fruit tree growth and branching habit since it affects both fruit production and training practices (Lauri and Lespinasse 1999). In addition, internode length and shoot conicity along with shoot slenderness have been shown to be the main determinants of shoot bending in apricot tree (Alméras et al. 2004). The lower the conicity, the higher the slenderness and the more the branches bend. Thus conicity and internode length could be used to predict branch propensity to bend, while cord bending could be a descriptor of branch flexion. However, because fructification is of major importance in the acquisition of branch and tree form, tree habit in the adult stage will result from interference between initial branch geometry and branch flexion process (Alméras et al. 2004). Thus, phenotyping trees from the first year of growth could provide information concerning the relative importance of the initial branch geometry and fructification in the variability of adult tree habit.

With regard to the branching process, many variables measured on the trunks showed heritability values greater than 0.3. These results are consistent with those found in Telamon x Breaburn 1-year-old apple tree hybrids and with the clustering of this progeny

based mainly on sylleptic branching (De Wit et al. 2002). The number of axillary shoots has several advantages in addition to its high heritability value: a significant genetic correlation with all topological variables, and it is easier to measure than other branching variables. At the axillary shoot level, branching at order 3 was also shown to be a relevant descriptor of architectural variability since it had a high heritability value and was poorly correlated with branching on trunks. This variable had a considerable weight in tree partitioning, since it was the only variable involved in the discrimination of the partition in two clusters. In fruit trees, the development of sylleptic shoots along the trunk in the early stage of tree development (in nursery), is considered as an advantage for young tree establishment (Wertheim 1978). Plant growth regulators (mostly including a cytokinin effect) are often applied in order to produce feathered trees which have a potential for early cropping (Miller 1988; Elfving and Visser 2005). In addition, the number of sylleptic shoots in young pear cultivars has been shown to be related to the length of the juvenile period (Costes et al. 2004). Since sylleptic shoots mainly develop during early developmental years of tree life (Crabbé 1987), this trait is expected to be a potential early selection criterion provided its correlation with interesting agronomic behavior at adult stage is checked in apple progenies.

Presently, our results are being used to continue investigating the genetic determinants of the architectural traits on older and more complex trees, using a within-tree sampling strategy. Progeny phenotyping in the second year of growth is in the process and for a longer time step, until flowering and fruiting occurrence. These further investigations should provide information on the correlations between the variables selected in the present study, at early stages of tree development, with traits of agronomic interest, measured at adult stage.

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583

583 **TABLES**

584 **Table 1.** List of quantitative variables classified whether they are related to tree geometry
585 or topology, corresponding abbreviates and within-tree positions of the measurements
586 (trunks and long sylleptic axillary shoots – LSAS). Formula are detailed for calculated
587 variables.

Variable		**Formula**	**Trunks**	**LSAS**
Geometry				
Length (mm)	L	Summed on growth units	X	X
Mean internode length (mm)	IN_L	L / IN_N	X	X
Length of the longest internode (mm)	IN_L_max		X	X
Basis diameter (mm)	B_Dia		X	X
Top diameter (mm)	T_Dia		X	X
Mean diameter (mm)	M_Dia	(B_Dia + T_Dia) / 2	X	X
Slenderness	Slend	L / M_Dia	X	X
Conicity	Coni	(B_Dia – T_Dia) / L	X	X
Axis volume (cm^3)	Vol	L . (B_area^a + T_area^a) / 2	X	X
Cord (mm)	Cord			X
Basis angle (° from horizontal)	B_Ang			X
Top angle (° from horizontal)	T_Ang			X
Angular bending (°)	Ang_Bend	|B_Ang – T_Ang|		X
Cord bending	Cord_Bend	1 – (Cord / L)		X
Topology				
Growth				
Number of internodes	IN_N		X	X
Branching				
Number of axillary shoots	Nb_AS		X	X
Number of long shoots	Nb_L		X	X
Number of brindles	Nb_B		X	X
Number of spurs	Nb_S		X	X
Percentage of branching nodes	%AS	Nb_AS / IN_N	X	X
Branching by length unit	Nb_AS/L	Nb_AS/ L	X	X
Branching zone	Br_Z	($Last\_AS^b$ – $First\_AS^b$) + 1	X	X
Branching density	Br_D	Nb_Ax / Zone_ramif	X	X

588 [a] $B\_area = \pi (B\_Dia / 2)^2$, $T\_area = \pi (T\_Dia / 2)^2$

589 [b] First_AS = rank from the basis of the first branching node, Last_AS = rank from the basis

590 of the last branching node

591

Table 2. Individual broad sense heritability values (h^2b) with confidence interval (CI) indicated into brackets for variables considered on both trunks and long sylleptic axillary shoots (LSAS; for variable abbreviates see Table 1).

Variables	Trunks		LSAS	
	h^2_b	CI (95 %)	h^2_b	CI (95 %)
Geometry				
L	0.38	[0.21, 0.56]	0.09	[0, 0.30]
IN_L	0.30	[0.12, 0.48]	0.49	[0.30, 0.68]
IN_L_max	0.24	[0.06, 0.42]	0.57	[0.41,0.74]
B_Dia	0.10	[0, 0.28]	0.12	[0,0.31]
T_Dia	0.14	[0, 0.32]	0.24	[0.04, 0.44]
M_Dia	0.10	[0, 0.27]	0.14	[0, 0.33]
Slend	0.29	[0.11, 0.48]	0.28	[0.06, 0.49]
Coni	0.19	[0.01, 0.37]	0.40	[0.21, 0.59]
Vol	0.16	[0, 0.34]	0.12	[0, 0.32]
Cord			0.04	[0, 0.25]
B_Ang			0.16	[0, 0.38]
T_Ang			0.21	[0, 0.42]
Ang_Bend			0.27	[0.07, 0.47]
Cord_Bend			0.30	[0.08, 0.52]
Topology				
Growth				
IN_N	0.17	[0, 0.35]	0.18	[0, 0.40]
Branching				
Nb_AS	0.41	[0.23, 0.58]	0.54	[0.33, 0.74]
Nb_L	0.06	[0, 0.23]	0.08	[0, 0.25]
Nb_B	0.34	[0.16, 0.51]	0.30	[0.10, 0.50]
Nb_S	0.46	[0.29, 0.63]	0.56	[0.33, 0.78]
%AS	0.33	[0.15, 0.51]	0.49	[0.28, 0.71]
Nb_AS/L	0.43	[0.26, 0.61]	0.51	[0.31, 0.71]
Br_Z	0.26	[0.07, 0.44]	0.35	[0.15, 0.54]
Br_D	0	[0, 0.11]	0.17	[0, 0.38]

Table 3. Variance decomposition for variables measured on long sylleptic axillary shoots (LSAS): estimates of genotypic, within-tree, residual and total variances (for variable abbreviates see Table 1). Significance of the corresponding factors are indicated as follows: ns – non significant, * – significant ($0.01 < p \leq 0.05$), ** – highly significant ($p \leq 0.01$).

Variables	Variances			
	Genotypic	Within-tree	Residual	Total
Geometry				
L	1769.12 ns	14914.95 **	12809.53	29493.60
IN_L	1.73 **	1.04 **	1.83	4.61
IN_L_max	4.56 **	2.02 **	5.42	12.00
B_Dia	0.23 ns	1.08 **	1.24	2.55
T_Dia	4.26E-02 *	8.53E-02 **	0.10	0.23
M_Dia	0.10 ns	0.40 **	0.39	0.90
Slend	128.35 *	251.36 **	261.84	641.55
Coni	8.32E-07 **	8.43E-07 **	1.45E-06	3.12E-06
Vol	4.75 ns	23.89 **	19.54	48.18
Cord	660.27 ns	11347.07 **	9715.28	21722.63
B_Ang	23.29 ns	25.24 *	139.40	187.92
T_Ang	53.06 ns	81.70 *	368.99	503.75
Ang_Bend	82.09 *	120.89 **	359.22	562.20
Cord_Bend	6.79E-04 *	5.40E-04 *	2.10E-03	3.32E-03
Topology				
Growth				
IN_N	15.93 ns	60.12 **	64.81	140.86
Branching				
Nb_AS	1.46 **	0.38 ns	2.68	4.52
Nb_L	2.23E-03 ns	2.24E-03 ns	6.45E-02	6.90E-02
Nb_B	4.02E-02 **	5.53E-03 ns	0.26	0.31
Nb_S	1.27 **	0.33 *	1.75	3.35
%AS	4.91E-04 **	2.00E-04 *	9.59E-04	1.65E-03
Nb_AS/L	3.74E-06 **	1.26E-06 *	7.79E-06	1.28E-05
Br_Z	4.56 *	1.58 ns	32.95	39.09
Br_D	1.49E-02 ns	3.08E-02 *	0.15	0.19

Table 4. Genetic correlations between variables selected on the basis of their broad sense heritability value, measured on trunks and long sylleptic axillary shoots (LSAS; for variable abbreviates see Table 1). Significant correlations ($p \leq 0.05$) are in bold. Genetic correlations higher than phenotypic correlations are in italics.

		Trunk Variables							LSAS Variables								
		L	IN_L	IN_L_max	Slend	Nb_AS	Nb_S	Nb_AS/L	IN_L	IN_L_max	Slend	Coni	Ang_Bend	Cord_Bend	Nb_AS	Nb_S	%AS	Nb_AS/L
Trunk Variables	L	1																
	IN_L	***0.84***	1															
	IN_L_max	***0.63***	***0.66***	1														
	Slend	***0.72***	***0.58***	***0.40***	1													
	Nb_AS	*-0.17*	*-0.21*	*-0.24*	***-0.41***	1												
	Nb_S	*-0.11*	*-0.20*	*-0.19*	*-0.21*	***0.85***	1											
	Nb_AS/L	***-0.41***	***-0.40***	***-0.40***	***-0.55***	***0.95***	***0.80***	1										
LSAS Variables	IN_L	***0.55***	***0.66***	***0.60***	***0.42***	***-0.45***	***-0.38***	***-0.55***	1									
	IN_L_max	***0.48***	**0.55**	***0.60***	***0.36***	***-0.49***	***-0.43***	***-0.60***	***0.83***	1								
	Slend	**0.32**	*0.11*	*0.16*	*0.22*	0.01	*-0.11*	*-0.11*	0.20	*0.26*	1							
	Coni	-0.23	*-0.08*	*-0.19*	***-0.37***	*0.09*	*0.15*	*0.17*	*-0.13*	*-0.15*	***-0.70***	1						
	Ang_Bend	0.07	0.03	*-0.07*	*-0.15*	*-0.05*	*-0.12*	*-0.09*	0.24	0.15	**0.40**	0.01	1					
	Cord_Bend	0.07	*-0.11*	*-0.17*	*0.02*	-0.03	*-0.06*	-0.04	-0.01	-0.01	**0.41**	-0.14	**0.68**	1				
	Nb_AS	***-0.28***	***-0.40***	*-0.26*	*-0.25*	*0.20*	0.22	*0.22*	*-0.05*	*0.12*	*0.26*	-0.02	*0.19*	*0.14*	1			
	Nb_S	***-0.29***	***-0.40***	***-0.28***	*-0.23*	0.20	0.23	0.21	*-0.06*	*0.12*	*0.23*	*-0.05*	*0.14*	*0.08*	***0.98***	1		
	%AS	***-0.32***	***-0.42***	***-0.28***	*-0.27*	*0.23*	0.24	*0.26*	*-0.05*	*0.09*	*0.21*	0.01	*0.15*	*0.09*	***0.99***	***0.97***	1	
	Nb_AS/L	***-0.33***	***-0.43***	***-0.30***	***-0.28***	*0.25*	0.26	***0.29***	*-0.09*	*0.05*	*0.21*	0.02	*0.13*	*0.09*	***0.99***	***0.96***	***1.00***	1

602 **Table 5.** Characterization of partition P_6 composed of 6 clusters: number of trees by
603 cluster (N), diameter, separate and mean value for each selected variable measured on
604 trunks and long sylleptic axillary shoots (LSAS; for variable abbreviates see Table 1).
605 Diameter = $d(within)_{max}$, separate = $d(between)_{min}$; a, b, c, d = discrimination of the
606 clusters according to the Newman-Keuls test ($p \leq 0.05$).

Clusters		1	2	3	4	5	6
N		5	7	22	39	34	42
diameter		2.73	3.24	3.22	2.78	2.94	3.06
separate		1.34	0.68	0.44	0.18	0.38	0.18
Trunks	IN_L	13.63 (b)	14.03 (b)	15.00 (b)	14.41 (b)	16.82 (c)	12.14 (a)
	Nb_AS	16.80 (c)	10.14 (a, b)	11.95 (b)	21.82 (d)	9.38 (a, b)	6.02 (a)
	Coni	0.0086 (a)	0.0079 (a)	0.0108 (b)	0.0084 (a)	0.0079 (a)	0.0081 (a)
LSAS	Cord_bend	0.09 (a)	0.24 (b)	0.07 (a)	0.10 (a)	0.09 (a)	0.08 (a)
	Nb_AS	6.82 (b)	1.10 (a)	0.48 (a)	1.05 (a)	0.48 (a)	0.83 (a)

607

FIGURES CAPTION

Figure 1. Schematic representation of a tree with 2 growth units (GU) on the trunk and 3 sylleptic branching orders. Branching orders are 1 for the trunk, 2 for the branches born on the trunk and so on; long sylleptic axillary shoots (LSAS). Three geometrical variables measured on the LSAS are illustrated.

Figure 2. Individual broad sense heritability value variation with the number of long axillary sylleptic shoots (LSAS) described, for a selection of variables: Nb_AS (●), Coni (○), Cord_Bend (▼), Nb_B (Δ), Br_D (■), T_Ang (□) (for variable abbreviates see Table 1).

Figure 3. Schematic representation of progeny partition into six clusters with a typical tree representing each cluster. Variables involved in the definition of each cluster are mentioned above the graph with the variation direction indicated by + versus -, and the number of trees per cluster are mentioned below the graph (for variable abbreviates see Table 1; _tr or _as were added to abbreviates whether the variable was measured on trunks or long sylleptic axillary shoots).

Fig.1

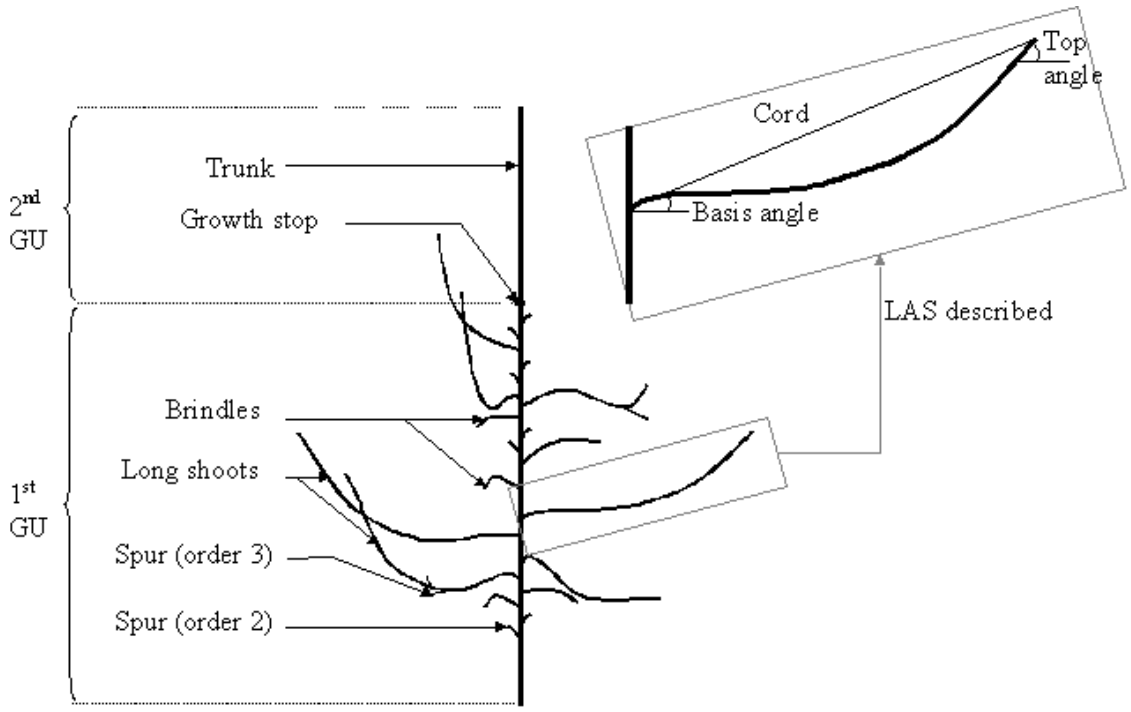

Top angle
Cord
Basis angle
LAS described
Trunk
Growth stop
2nd GU
Brindles
Long shoots
1st GU
Spur (order 3)
Spur (order 2)

Fig. 2

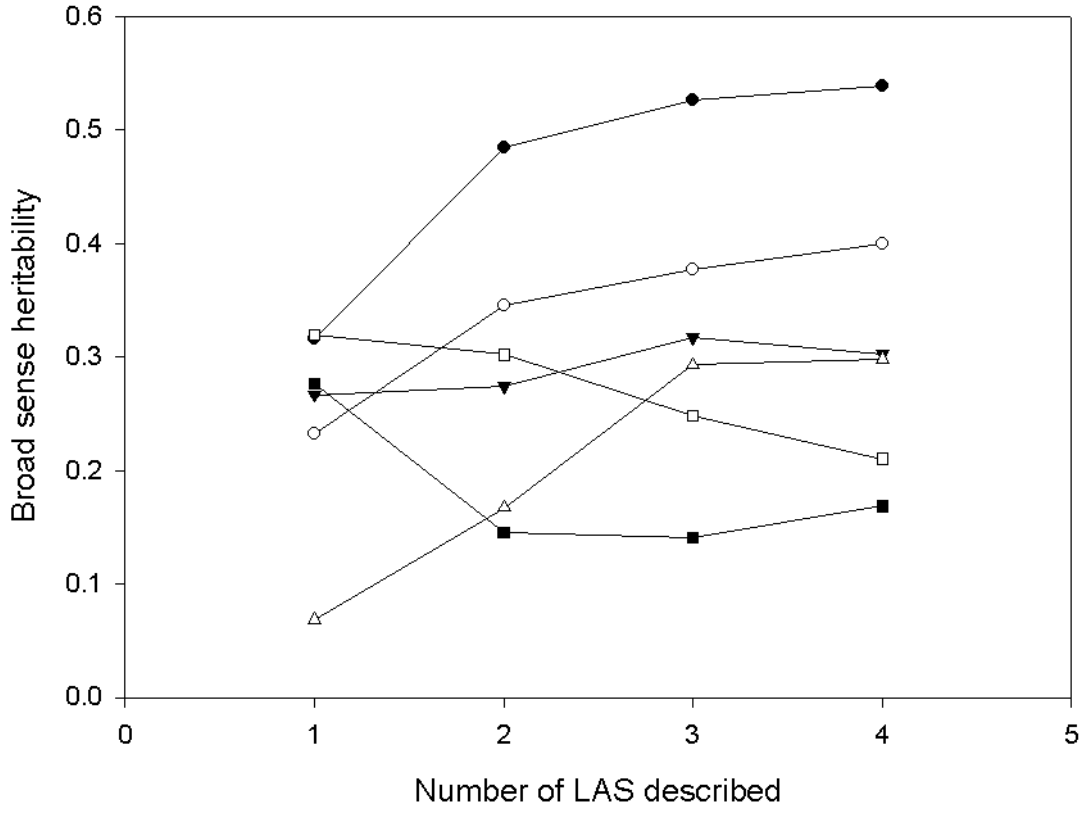
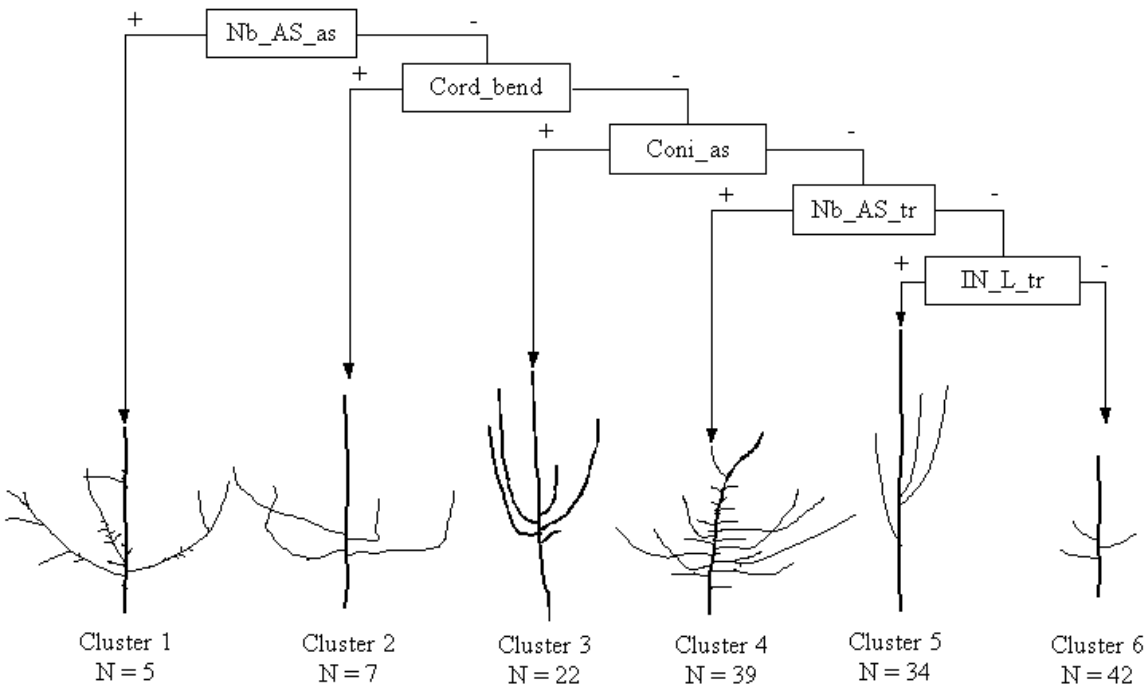

Broad sense heritability
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0
1
2
3
4
5
Number of LAS described

Fig. 3


Nb_AS_as
Cord_bend
Coni_as
Nb_AS_tr
IN_L_tr
+
-
Cluster 1
N = 5
Cluster 2
N = 7
Cluster 3
N = 22
Cluster 4
N = 39
Cluster 5
N = 34
Cluster 6
N = 42